

Spatial synchrony at the extremes: Tail-dependence in temperature drives tail-dependence in birds' spatial synchrony across North America

Shyamolina Ghosh¹ and Owen Petchey¹

¹University of Zurich

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Abstract

Environmental change is becoming synchronous across sites with frequent emergence of extremes in recent years, with alarming potential impacts on species' synchronous abundance over large scales. With 23 years of breeding bird survey data across North America, we found that some birds are becoming synchronously rare across sites, while others are becoming synchronously common. We evaluated the relative importance of two co-occurring mechanisms (environment-driven and dispersal-driven) to explain such spatial synchrony in extreme low or high abundance (i.e., tail-dependent synchrony). We found that spatial synchrony in temperature extremes (i.e., tail-dependence in climate) was the major driver for birds' tail-dependent spatial synchrony up to 250 Km. In addition, temperature extremes and dispersal trait both favored synergistically some species making them synchronously common across sites. In a rapidly changing environment, these findings highlight the importance of considering synchronized climatic extremes to assess species' tail-dependent spatial synchrony across large scale.

1 **Title:** Spatial synchrony at the extremes: Tail-dependence in temperature drives tail-dependence
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4 **Authors and emails:**

5 Shyamolina Ghosh^{1*}(ghoshshyamolina89@gmail.com),

6 Owen L. Petchey¹(owen.petchey@ieu.uzh.ch)

7

8 **Affiliations:**

9 1. Department of Evolutionary Biology and Environmental studies, University of Zurich;
10 Winterthurerstrasse 190, 8057 Zurich, Switzerland

11 ***Name, mailing address, email, phone number of corresponding author:**

12 Dr. Shyamolina Ghosh

13 Senior researcher (oberassistentin)

14 Department of Evolutionary Biology and Environmental Studies, University of Zurich

15 Winterthurerstrasse 190, 8057 Zurich, Switzerland

16 Phone (+41) 779567848, email ghoshshyamolina89@gmail.com

17

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35 2014); Birds of the World: (Billerman *et al.* 2022); BirdTree: <https://birdtree.org/>). Analyses
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37 in Zenodo (<https://doi.org/10.5281/zenodo.10119915>).

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47 Abstract

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49 extremes in recent years, with alarming potential impacts on species' synchronous abundance
50 over large scales. With 23 years of breeding bird survey data across North America, we found
51 that some birds are becoming synchronously rare across sites, while others are becoming
52 synchronously common. We evaluated the relative importance of two co-occurring mechanisms
53 (environment-driven and dispersal-driven) to explain such spatial synchrony in extreme low or
54 high abundance (i.e., tail-dependent synchrony). We found that spatial synchrony in temperature
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57 synergistically some species making them synchronously common across sites. In a rapidly
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70 Introduction

71 Understanding spatio-temporal patterns in the abundance of natural populations has been
72 a long-standing interest for ecologists (Gaston & Blackburn 2000). Spatial synchrony - i.e., the
73 correlated fluctuation in metapopulation abundances from geographically distinct sites - is a
74 ubiquitous spatio-temporal pattern widely observed in many taxa (Bjørnstad *et al.* 1999;
75 Liebhold *et al.* 2004). Spatial synchrony in metapopulations can arise due to diverse factors
76 (Haynes & Walter 2022), including similar responses to correlated environmental drivers- the
77 mechanism known as “Moran effects” (Moran 1953; Hansen *et al.* 2020), as well as dispersal
78 within metapopulations (Goldwyn & Hastings 2008; Abbott 2011), and effects of synchronized
79 or mobile predators (Haynes *et al.* 2009; Vasseur & Fox 2009). Studying spatial synchrony for a
80 given species helps ecologists to understand aggregate-level variability, species’ vulnerability,
81 and spatial prioritization of conservation management (Heino *et al.* 1997; Koenig & Liebhold
82 2016; Allen & Lockwood 2020; Walter *et al.* 2021; Yang *et al.* 2022).

83 Growing evidence indicates that on one hand, extreme climatic events are becoming
84 more frequent (La Sorte *et al.* 2021; Li *et al.* 2021) and on the other hand, spatial synchrony in
85 metapopulations increases because of increasing spatial synchrony in climatic conditions
86 (Koenig 2002; Kahilainen *et al.* 2018). These phenomena create considerable concern for species
87 conservation and lead us to consider the impact of spatial synchrony on population viability
88 beyond the usual approaches. The usual approach measures pairwise synchrony through
89 correlation between two fluctuating variables from two sites (variables could be two
90 metapopulation abundance time series, or could be two temperature time series) and then
91 compares synchrony in abundance and synchrony in temperature for evidence of the
92 “Moran-effect”. However, when using correlation to measure pairwise synchrony, the influence

93 of extremes, either in terms of population size or in climatic events, may be missed. Moreover,
94 extreme climatic events have an important effect on local to regional climatic changes and on
95 overall biodiversity change, because extremes can result in climatic conditions beyond the
96 tolerance range of species (Ummenhofer & Meehl 2017). Therefore, it is essential to investigate
97 linkages between spatial synchrony of species' populations and climatic conditions considering
98 the importance of climatic extremes for population extremes. We term this “synchrony at the
99 extremes”, and also “tail-dependence” since it concerns associations/dependencies in the tails of
100 the distributions of variables.

101 In simple words, measuring “tail-dependence” focuses on the tails (low or high end) of
102 the concerned distribution (e.g., for a joint distribution of population abundances from two sites),
103 rather than the middle part of it - which is the focus for a correlation-based approach. For the
104 same given correlation coefficient two metapopulations can show a variety of tail-dependence
105 (Fig. 1, symmetric tail: A1-A2 no tail-dependence; B1-B2: lower tail-dependence, and for
106 C1-C2: upper tail-dependence) with different implications for extinction risk. A lower tail (LT)
107 dependence indicates that populations are synchronously rare at both sites (i.e., their dynamics
108 are more similar when they have low abundance, Fig. 1, B1-B2). Whereas upper tail (UT)
109 dependence indicates that populations are synchronously abundant at both sites (i.e., their
110 dynamics are more similar when they are at peak abundance values through time, Fig. 1, C1-C2).

111 Recently, some local-scale studies showed the importance of “tail-dependence” (i.e.,
112 considering the synchrony among extreme values beyond the usual correlation coefficient) for
113 synchrony at the extremes (Ghosh *et al.* 2020b; Walter *et al.* 2022), stability (Ghosh *et al.* 2021),
114 and metapopulation extinction risk (Ghosh *et al.* 2020c). Since extinction risk is often related to
115 the size of the populations, the risk of regional- to global-scale extinction is increased due to

116 poor rescue effects if metapopulations are synchronously rare across sites (Ghosh *et al.* 2020c) as
117 shown in Fig. 1, B1-B2. On the contrary, lower extinction risk is expected if species are
118 synchronously common across sites (Fig. 1, A1-A2) or overall synchronous with symmetric tail
119 dependence (Fig. 1, C1-C2). A recent regional study (Walter *et al.* 2022) shows nonlinear
120 threshold-like relationship between population abundance and its environmental driver as a
121 possible mechanism explaining both type of tail-dependent spatial synchrony in population
122 abundance, and is consistent with other theoretical and empirical studies that indicate
123 tail-dependence can arise from threshold like phenomena in ecology (Ghosh *et al.* 2020a, b).

124 Here, we provide an analysis of long-term dynamics (1997-2019) of bird species
125 abundances, temperature and precipitation across North America to explore effects of extreme
126 climates on birds' spatial synchrony (>250 species, >5700 sites). We focused on birds because
127 they are often considered as important for ecosystem service and excellent indicators of
128 environmental health (Furness *et al.* 1993; Jetz *et al.* 2022; Cohen & Jetz 2023; Ramos *et al.*
129 2023), and because of data availability. We first investigated if Q1) species show a particular
130 type of dependence pattern across sites (e.g., lower, upper, or no spatial tail-dependence) and if
131 so, then Q2) what would be the driving mechanism for such patterns in tail-dependence (Fig. 2).
132 We also checked if there is any relationship between species' tail-dependent synchrony and their
133 diet or IUCN status. We then proposed a mechanism that extends the classic Moran effect by
134 considering "tail-dependence", i.e., that tail-dependence (lower or upper) in spatial synchrony of
135 an environmental driver will lead to tail-dependence (lower or upper) in spatial synchrony of
136 birds' abundances. For example, we predict lower tail dependence (LTD) in spatial synchrony for
137 precipitation (i.e., when low rainfall across sites) will lead to LTD in metapopulation synchrony
138 (i.e., metapopulations synchronously rare). Whereas we predict that upper tail dependence

139 (UTD) in temperature spatial synchrony would cause LTD in abundances (i.e., widespread high
140 temperatures cause widespread low abundances). Therefore, we hypothesize and explore
141 whether high temperature and low precipitation (hot-dry extreme climates) are associated with
142 LTD in metapopulation synchrony for some species (Fig. 2 - Case I) and UTD for others (Fig. 2 -
143 Case II).

144 Since dispersal can also influence spatial synchrony, we hypothesized that species with
145 greater dispersal ability would be synchronously common across sites. Therefore, we explore
146 Q3) is tail-dependent synchrony in birds' abundance associated with tail-dependent synchrony in
147 climatic variables or with the value of dispersal associated traits (e.g., Hand-Wing Index, HWI)
148 (Germain *et al.* 2023) (Fig. 3)? Furthermore, we examine the relative importance of such
149 dispersal trait-mediated pathways and climate driven pathways (Fig. 3). We examine with Figure
150 3 to explain why some species show LTD in synchronous spatial abundance (i.e., rare across
151 sites) where other species show UTD.

152

153 **Materials and Methods**

154 **Data**

155 *Abundance data*

156 We used 23 years (1997-2019) of the North American Breeding Bird Survey (BBS)
157 dataset. It contains information of species level bird counts in around 62 states, provinces, or
158 territories in the U.S. and Canada (Pardieck *et al.* 2020). BBS data originally has been collected
159 since 1966, but in 1997 there was a change from subjective (manual) to objective process to
160 evaluate survey-quality. Therefore, we only considered data 1997 onwards to maintain

161 consistency. Sampling routes were ~ 39.2 Km long with 50 stops placed at ~800m intervals and
162 mostly sampled during breeding season (June). We used the total count across these 50 stops for
163 a given route and for a given species. 1,227 routes (sites) and 652 species were sampled at least
164 once during the study period. Finally, the species list was reduced to 373 species based on the
165 criterion that they were sampled at least at two sites for a minimum of 20 years. Species-level
166 abundance time series data were used to compute spatial synchrony for birds at their extreme low
167 or high abundance.

168 *Climate data*

169 For climate variables, we used annual temperature and precipitation data (averaged across
170 12 months data, extracted from CHELSA, version 2.1 (Karger *et al.* 2017), for a given year, ~1
171 Km resolution) for the same 23 years at those 1227 sampling sites. As precipitation data were not
172 available for all months of 2019, so we considered timespan 1997-2018 for precipitation data.
173 This annual climate time series data were used to compute spatial synchrony for precipitation
174 and temperature at their extreme values.

175 *Trait data*

176 We gathered information about species' diet type (total 5 categories: invertebrates,
177 omnivore, plants & seeds, vertebrates & fish & carrion, fruit & nectar), mainly from the
178 *EltonTraits* database (Wilman *et al.* 2014), and if for some species diet type was not found there,
179 then we also searched on Birds of the World (Billerman *et al.* 2022). Species' morphological
180 traits used in this study were extracted from the AVONET database (Tobias *et al.* 2022). We used
181 the trait hand-wing index (HWI) which is considered as a proxy for birds' dispersal ability and
182 determinant of their geographical range-size (Sheard *et al.* 2020).

183 *Quantifying (tail-dependent) spatial synchrony*

184 First we detrended each species' abundance time series to remove linear temporal trends
185 using “detrend” function from *pracma* R-package (Borchers & Borchers 2022), otherwise it
186 could lead to spurious correlations. For a given species and for any two positively correlated
187 (overall synchronous) detrended abundance time series taken from two sites, we then computed
188 spatial synchrony at the extremes (i.e., tail-dependence) in the following ways. We computed
189 *partial Spearman correlation* (Ghosh *et al.* 2020a) for the simultaneous low values, Cor_l (or
190 high values, Cor_u), of two detrended metapopulation abundance time series. See section
191 “*Computing partial Spearman correlation (Cor_l , Cor_u)*” below for a detailed description.

192 The difference $Cor_l - Cor_u$ indicates if a species is predominantly synchronously rare
193 ($Cor_l - Cor_u > 0$) or predominantly synchronously common at both sites ($Cor_l - Cor_u < 0$). We
194 repeated this analysis for all pairwise combinations of sampling sites for a given species that
195 were within a distance of 250 Km. There were 263 species selected in total within that 0-250 Km
196 distance category. The choice of 250 Km radius was supported by the finding that both Cor_l and
197 Cor_u dropped rapidly beyond that distance (Fig. S1).

198 For a given species sampled at S number of sites, we calculated the overall lower tail
199 dependence $L = \sum_i (Cor_l - Cor_u)$ where i is the index for site-pair having $Cor_l > Cor_u$, and overall

200 upper tail dependence $U = \sum_j (Cor_l - Cor_u)$ where j is the index for site-pair having $Cor_l < Cor_u$.

201 Throughout the manuscript, we will mention species as “lower tail-dependent” if the proportion
202 of lower minus upper tail-dependence, $f_{TD}^{abundance} (= f_{TD,L}^{abundance} - f_{TD,|U|}^{abundance})$, is positive, and

203 “upper tail-dependent” if $f_{TD}^{abundance}$ is negative, where $f_{TD,L}^{abundance} = \frac{L}{L+|U|}$, and
 204 $f_{TD,|U|}^{abundance} = \frac{|U|}{L+|U|}$. Subscript TD is short-hand notation for tail-dependence. The maximum
 205 value of $f_{TD}^{abundance}$ is 1 when $f_{TD,|U|}^{abundance} = 0$; this occurs when across sites synchrony happens
 206 only at low. The minimum value of $f_{TD}^{abundance}$ is -1 when $f_{TD,L}^{abundance} = 0$; this occurs when across
 207 sites synchrony happens only at high values). A $f_{TD}^{abundance}$ of zero value indicates no
 208 tail-dependent synchrony (i.e., $f_{TD,L}^{abundance} = f_{TD,|U|}^{abundance}$) happens among metapopulation
 209 abundance across sites (e.g., see Fig. 1, A1-A2).

210 To compute the spatial synchrony for climate extremes (precipitation, P , and temperature,
 211 T), we followed a similar approach as computing spatial synchrony at extreme abundances. We
 212 first detrended the climate time series, and then within 0-250 Km of between-sites distance
 213 category, calculated the proportion of tail-dependence in climate time series as
 214 $f_{TD}^{climate,P} = f_{TD,L}^{climate,P} - f_{TD,|U|}^{climate,P}$ and $f_{TD}^{climate,T} = f_{TD,L}^{climate,T} - f_{TD,|U|}^{climate,T}$, where T is
 215 temperature and P is precipitation.

216 ***Computing partial Spearman correlation (Cor_l , Cor_u)***

217 Partial Spearman correlation approach uses “copula” - a statistical tool that computes
 218 dependence between any two variables at their simultaneous low or high ranks (Ghosh *et al.*
 219 2020a), and recently has been used in ecological field to measure tail-dependent synchrony
 220 (Ghosh *et al.* 2020b, c, 2021). Ranking individual time series makes the marginal distribution
 221 uniform and thus helps to extract the dependence information for the joint distribution (Sklar
 222 1959). For example, if you start with two metapopulation abundance time series

223 $\{x_t, y_t\}; t = 1, \dots, n$, then the corresponding copula would be
224 $\{u_t, v_t\} = \{\text{rank}(x_t), \text{rank}(y_t)\}/(n + 1)$, so that the range of the ranked time series
225 variables $\{u_t, v_t\}$ lies within 0 to 1. Here, lowest value would get rank 1 whereas highest value
226 would get a rank n . Following (Ghosh *et al.* 2020a), one then can calculate the dependence
227 between $\{u_t, v_t\}$ for the lower half of the unit box (i.e., for the points lying below the line
228 $u + v = 1$) as Cor_l and for the upper half of the unit box (i.e., for the points lying above the
229 line $u + v = 1$) as Cor_u . In our study with a minimum of 20-years analysis, we chose this 50%
230 threshold to compute synchrony at the extremes (or tail-dependence), but with more
231 data-availability one could use 75% or 90% threshold to define the extremes.

232 ***Model-selection based approach with SEM considering phylogeny***

233 We considered the model (Fig. 3) to explain the variation in proportion of tail-dependent
234 synchrony in species abundance, $f_{TD}^{abundance}$. In this model, we hypothesized $f_{TD}^{abundance}$ would be
235 driven both by the patterns in $f_{TD}^{climate}$ and dispersal trait HWI. To test which hypothesized path
236 would best explain the variation in $f_{TD}^{abundance}$, we used a structural equation modeling (SEM)
237 considering species' phylogenetic relationships. For the phylogeny, we subsampled 1,000
238 'Ericson All Species: a set of 10,000 trees with 9993 OTU each' trees pruned for our set of
239 species (N=253 species matched from BirdTree database, source: <https://birdtree.org/subsets/>
240 (species-level information is provided in the "DATA/BirdTree" folder of the code repository).
241 All 1,000 trees were well-behaved (i.e., rooted, binary, ultrametric, and strictly bifurcating).
242 Then, we made a consensus tree from those 1,000 trees to look primarily if there were any
243 pattern for $f_{TD}^{abundance}$ or for trait, HWI (Fig. S2, A-B). Visually, we did not find any pattern in

244 $f_{TD}^{abundance}$ and this was also supported by non-significant and weak phylogenetic signal (mean
245 Pagel's $\lambda \sim 0.12$). We did, however, find significantly strong phylogenetic signal (mean Pagel's λ
246 ~ 0.993 , all p -values < 0.00001) in the trait HWI for those 1,000 trees (Fig. S2, C), which is also
247 clearly observed in that consensus tree (Fig. S2, B). Function “*phylosig()*” from *phytools*
248 R-package (Revell 2012) was used to quantify Pagel's λ . Finally, we did a phylogenetic path
249 analysis (PPA) (Gonzalez-Voyer & von Hardenberg 2014), for that model as hypothesized in Fig.
250 3. We implemented PPA for our data with the *phylopath* R-package (van der Bijl 2018).

251

252 Results

253 We found tail-dependence in birds' spatial synchrony for 263 species considered (Fig. 4).
254 Of the 263 species, 127 species showed lower tail-dependent spatial synchrony (i.e., species
255 were simultaneously having low abundance value across sites, $f_{TD,L}^{abundance} > f_{TD,|U|}^{abundance}$ in Fig.
256 4, A) and 136 species showed upper tail-dependent spatial synchrony (i.e., species were
257 simultaneously having high abundance value across sites, $f_{TD,L}^{abundance} < f_{TD,|U|}^{abundance}$ in Fig. 4, B).
258 This observation confirmed (Q1) of Fig. 2 that, indeed, birds' across north America showed
259 tail-dependence patterns in spatial synchrony.

260 We did not find any particular tail-dependence patterns based on species' diets and IUCN
261 status. Species appeared to be synchronously rare (N= 127, Fig. 4, A) and as well as common
262 (N=136, Fig. 4, B) in all of the five diet categories considered. Interestingly, Fig. 4, A showed
263 even if some species were listed as “Least Concerned, LC” as per IUCN status, some of those
264 species had synchronously rare abundance.

265 We found that tail-dependent spatial synchrony in climate (particularly, in temperature)
266 was driving the tail-dependent spatial synchrony in birds (Fig. 5), answering (Q2) of Fig. 2.
267 Lower tail-dependent and upper tail-dependent species showed opposite types of response to
268 synchrony in climate nullifying the significant patterns when considered altogether (Fig. S3).
269 Patterns were clearer when we considered two groups separately (Fig. S4). Proportion of
270 tail-dependent spatial synchrony in temperature, $f_{TD}^{climate, T}$, appeared as the common significant
271 driver for the proportion of tail-dependent spatial synchrony in birds' abundance, $f_{TD}^{abundance}$,
272 making lower tail-dependent species rare across sites as high temperature prevailed across those
273 sites (Fig. S4, B) and leaving upper tail-dependent species common across sites (Fig. S4, D).

274 Phylogenetic path analysis showed the climate-driven pathway as relatively more
275 important than the dispersal-mediated pathway to explain variation in $f_{TD}^{abundance}$ for both group
276 of species (absolute regression coefficients for pathway i were greater than pathway ii, Fig. 5),
277 answering (Q3).

278 For lower tail dependent group, species were synchronously rare across sites because of
279 simultaneous high temperature across sites (i.e., spatial synchrony in high temperature extremes).
280 Pathway (i) of Fig. 5, A with regression coefficient = -0.31 shows more negative values of
281 $f_{TD}^{climate, T}$ had higher association with more positive values of $f_{TD}^{abundance}$ (also see Fig. S4, B).
282 Species that were synchronously rare had higher HWI (pathway iv, regression coefficient = 0.12,
283 increasing HWI making $f_{TD}^{abundance}$ more positive), though the effect was non-significant (Fig. 5,
284 B). The dispersal-mediated pathway was also weaker compared to the climate-driven pathway.
285 Clearly, species showed simultaneously low abundance across sites because of more negative

286 impact on $f_{TD}^{abundance}$ due to tail-dependent spatial synchrony in high temperature (i.e., high T
287 across sites).

288 For the upper tail-dependent group of species ($f_{TD}^{abundance} < 0$ in Fig. 5, C), there were two
289 significant pathways affecting $f_{TD}^{abundance}$: climate-driven (pathway i) and dispersal-mediated
290 (pathway ii). Both pathways favored species' simultaneously high abundance across sites, with
291 the climate-driven pathway being more important. Simultaneous high temperature across sites
292 increased spatial synchrony in abundance (regression coefficient = 0.27, more negative values of
293 $f_{TD}^{climate, T}$ had higher association with more negative values of $f_{TD}^{abundance}$, also see Fig. S4, D).
294 Species that could easily disperse (i.e., better dispersal ability with high HWI) were
295 synchronously abundant across sites (regression coefficient = -0.16, increasing HWI making
296 $f_{TD}^{abundance}$ more negative).

297 We present the model and results considering temperature as the only climatic driver for
298 the following reasons. First, we can see that even for simple regression, precipitation was not a
299 significant predictor for both group of species (Fig. S4). Second, we feel it is better to not include
300 two correlated climatic predictors into a single model to avoid the collinearity issue.

301

302 Discussion

303 Overall, we found birds across North America showed tail-dependence in spatial
304 synchrony (becoming synchronously rare or common across sites). This large-scale pattern (up to
305 250 Km) was driven by synchrony in extreme climate and by a dispersal-related trait, where
306 tail-dependent spatial synchrony in temperature appeared to be more important.

307 These findings are practically significant in at least three important ways. First,
308 tail-dependence patterns in metapopulation ecology are known to be linked to extinction risk
309 (Ghosh *et al.* 2020c). Hence our findings highlight species (from the lower-tail dependent group)
310 at higher risk than is estimated in usual analysis. Furthermore, many species, which are listed as
311 “least-concerned” in IUCN status appeared in that lower tail-dependent group. It could be useful
312 to include tail-dependent spatial synchrony in future assessments of a species vulnerability.

313 Second, here we proposed an extension of classic Moran-effect (i.e., environmental
314 correlation drives correlation between metapopulation abundance) beyond the usual correlation
315 based approach. Our finding of such large scale tail-dependence patterns in spatial synchrony for
316 both climates and abundance also resonates with similar findings from global patterns in
317 environmental synchrony that can explain classic Moran effect (Koenig 2002). We demonstrated
318 that tail-dependent spatial synchrony in climatic variables drive large-scale tail-dependent spatial
319 synchrony patterns in birds’ abundance. It could be caused by resource limitation or extreme
320 environmental conditions that limit some species’ growth but benefit others. This finding
321 highlights the underlying nonlinearity (beyond linear correlation) as a mechanism to understand
322 how tail-dependence in climate synchrony translates into tail-dependence in metapopulation
323 synchrony, as found by a recent study (Walter *et al.* 2022).

324 Third, we attempted to disentangle the relative contributions of tail-dependent spatial
325 synchrony in climate and of dispersal. Dispersal and correlated environmental fluctuation
326 (“Moran effect”) are both known as important drivers for spatial synchrony (Liebhold *et al.*
327 2004) and their contribution often depends on spatial scale (Lande *et al.* 1999), environmental
328 correlation being of greater importance at larger scales (Peltonen *et al.* 2002). For tail-dependent
329 spatial synchrony in abundance, we found similar results: large scale patterns (~250 Km apart)

330 are driven mostly by tail-dependent spatial synchrony in temperature. To our knowledge, this is
331 the first study to assess the contribution of two co-occurring mechanisms for tail-dependent
332 metapopulation synchrony.

333 For both groups of species, we found environmental synchrony was the main driving
334 factor (Fig. 5, A and C). For the species with lower tail-dependence, high temperature across
335 sites imposed a stressed environment for them making synchronously rare. Whereas the species
336 with upper tail-dependence we found the synergistic effect of environmental and trait-based
337 selection on tail-dependent spatial synchrony - i.e., both high dispersal ability and high
338 temperature across sites made them synchronously abundant. Though in our study, we did not
339 quantify the dispersal directly as it requires additional data, for example, by tracking individuals.
340 Rather, we used a trait-based approach with the expectation that species with traits for better
341 dispersal ability (higher HWI) should show higher spatial synchrony.

342 Our study offers an improved understanding of the underlying mechanism of how
343 spatio-temporal patterns in metapopulation synchrony for North-American birds are shaped by
344 climatic synchrony at the extremes, and the approach could be generalized to any taxa. We
345 provide a mechanism beyond the classic “Moran effect”, to explain such patterns and also
346 compare its importance with respect to an alternate dispersal-mediated (or trait-mediated)
347 pathway. We believe our findings will encourage further exploration about detecting the role of
348 environmental filtering and natural selection to understand macro-scale patterns in the field of
349 ecology and evolutionary biology.

350 Future studies could focus on two directions. First, exploration of another possible
351 mechanistic explanation for tail-dependent synchrony in metapopulation abundances: either by

352 a bottom-up effect or by a top-down effect in multi-trophic food web context. In a bottom-up
353 approach, due to limited food resources in the primary producer levels, the consumer could be
354 synchronously rare (LT dependence) across sites. A similar result has been found for red
355 squirrels' meta-population synchrony over a large scale that was mainly driven by synchrony in
356 their primary resource: spruce cones (Turkia *et al.* 2020). In a top-down approach, one could test
357 if tail-dependent spatial synchrony in a prey population happens because of extreme pressure of
358 predation or not. Synchronized predation is a known factor causing spatial synchrony in prey
359 populations (Ims & Andreassen 2000; Vasseur & Fox 2009), and a recent study showed
360 behavioral synchrony amplified in a group of prey populations due to fear of predation (Aguilar
361 de Soto *et al.* 2020). Tail-dependence has not been studied in this context.

362 Second, in addition to natural selection for disadvantageous or beneficial dispersal trait
363 values, another possibility is that dispersal could be limited by habitat fragmentation due to
364 land-use change (Moore *et al.* 2008). In the current study, we did not consider the anthropogenic
365 impact on birds' dispersal ability or on the tail-dependent synchrony in climatic extremes. As
366 land-use change and climate change are coupled together (Oliver & Morecroft 2014), and
367 globally climatic extremes are projected to increase due to anthropogenic pressure (Zhou *et al.*
368 2023), considering both aspect in explaining tail-dependent spatial synchrony for abundance
369 would be a logical avenue for future study (Holyoak & Heath 2016).

370 In sum, we found considerable tail-dependent spatial synchrony (for abundance) in bird
371 population dynamics. We evaluated the relative importance of co-occurring mechanisms
372 (tail-dependent climatic variables and dispersal) to find out that it was the environmental effects
373 which prevailed on large-scale patterns. Our study is possible because of long-term data (a
374 minimum of 20 years) availability for birds' count, climate time series, and species-level traits

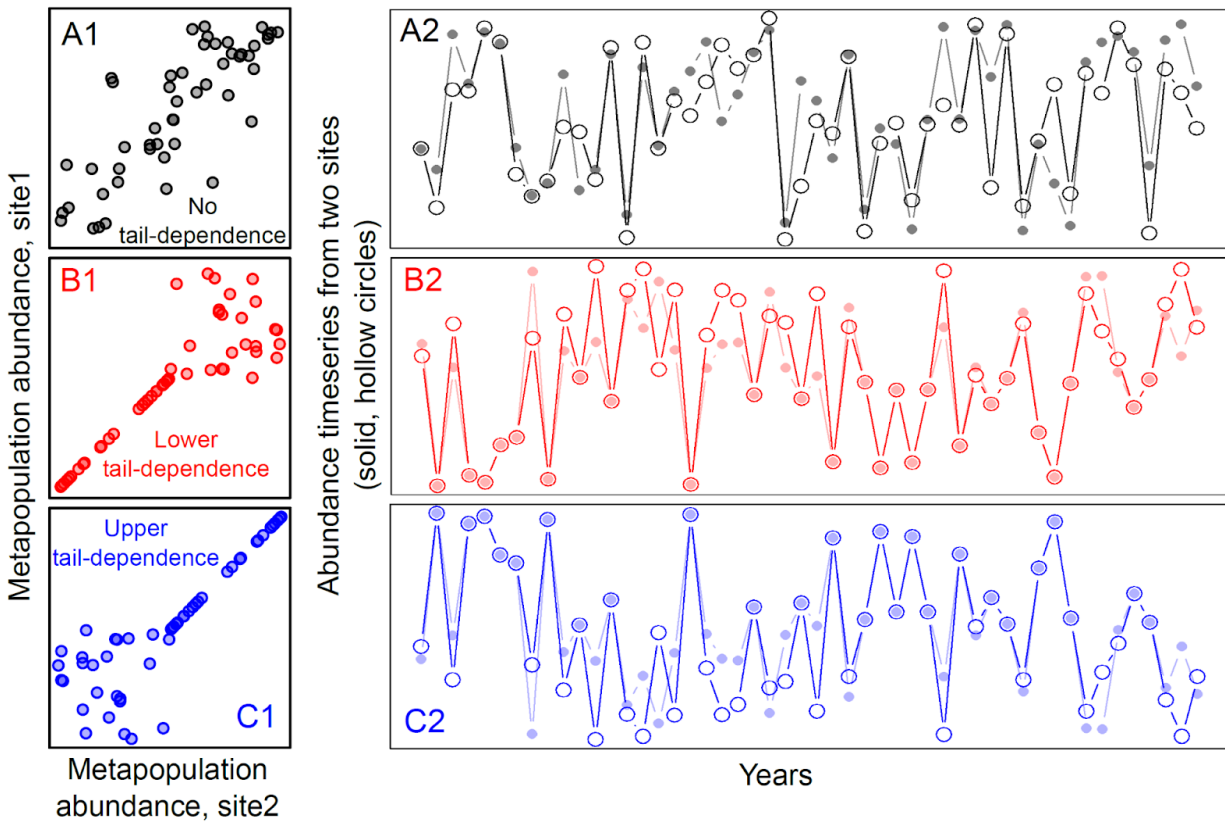
375 information. Long-term monitoring data are immensely important in ecological research (Willis
376 *et al.* 2007), including detecting the effect of extremes (i.e., tail-dependence) and to evaluate the
377 effect of natural selection on birds' traits in the context of present study. We hope that with the
378 increasing accessibility of long-term monitoring data, scientists will continue such mechanistic
379 exploration on spatio-temporal macroecological patterns.

380

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384 **Competing interests** The authors declare that they have no competing interests.

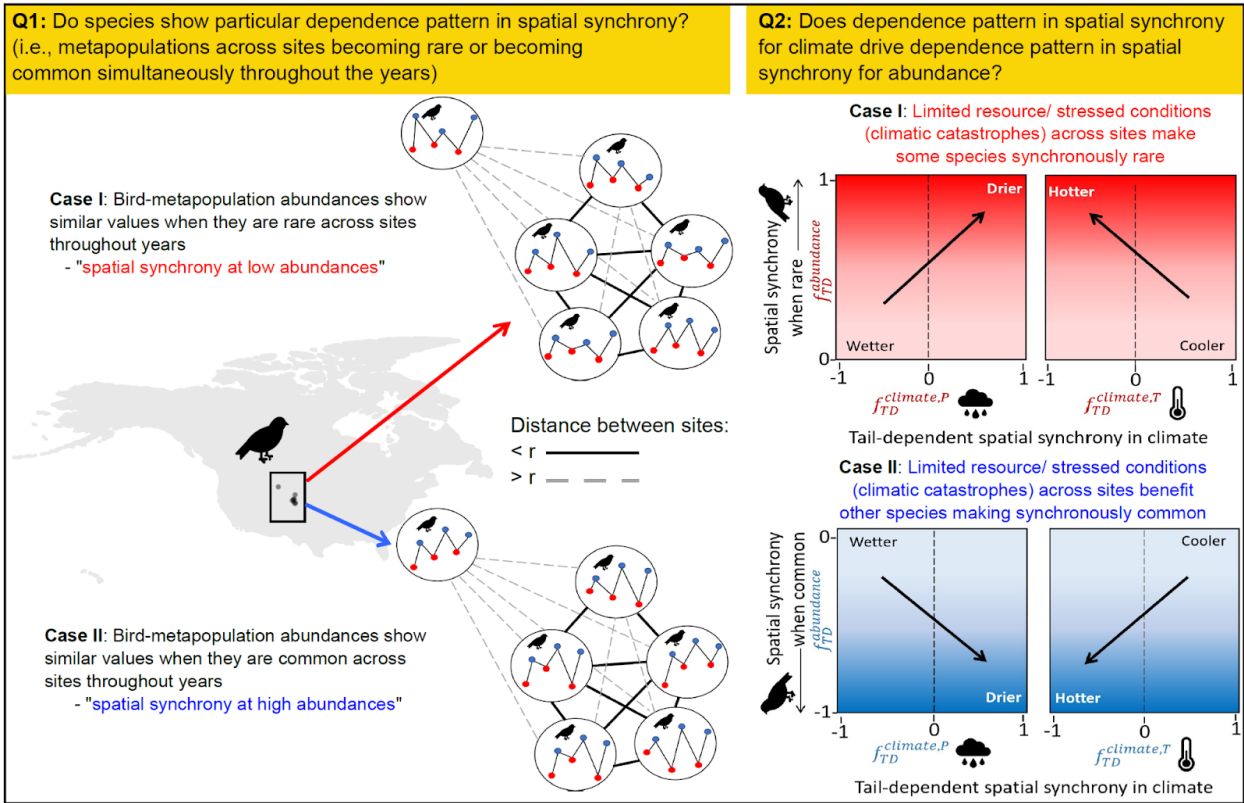
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388 **Figure 1:** Visualization of tail-dependent spatial synchrony. Left panels (A1-C1) show the
 389 copula-plot (scatterplot of normalized ranks) for two metapopulation sites having the same
 390 spearman correlation, but zero, positive (lower) and negative (upper) tail-dependent synchrony,
 391 respectively. Right panels (A2-C2) show metapopulation abundance time series from two sites
 392 corresponding to their left panel analog. One can see for asymmetric copula like B1 and C1,
 393 mostly all the hollow and solid circles exactly coincide in B2 and C2 for their troughs and peaks,
 394 respectively.

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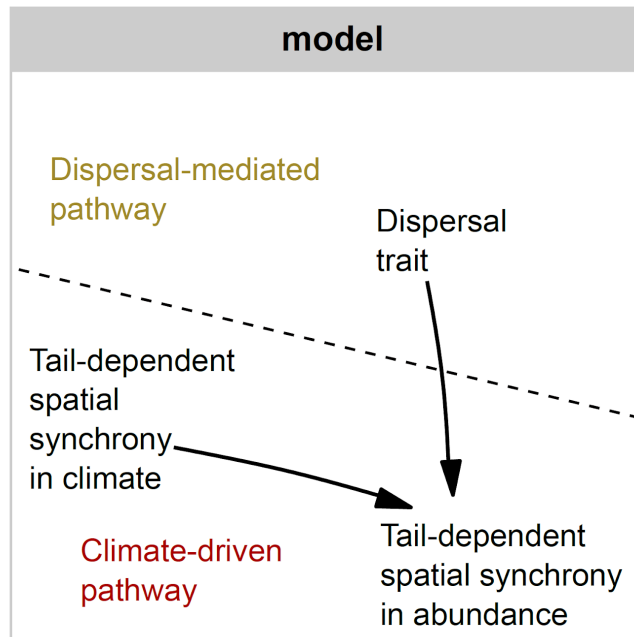


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397 **Figure 2:** Conceptual figure showing the emergence of lower tail-dependent (Case I: spatial
 398 synchrony at low abundances) and upper tail-dependent (Case II: spatial synchrony at high
 399 abundances) spatial synchrony in species' abundance which is driven by tail-dependent spatial
 400 synchrony in the climatic drivers. For spatial synchrony at low abundance in Case I, red points
 401 are showing similar fluctuation in the abundance time series across metapopulation sites,
 402 whereas for spatial synchrony at high abundance in Case II, blue points are showing similar
 403 fluctuation in the abundance time series across sites. Spatial synchrony would be high among
 404 sites which are closer ($<r$, solid lines).

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Q3: Which pathway is more important in driving tail-dependent spatial synchrony in abundance?
Climate-driven pathway or dispersal-mediated pathway?



406

407 **Figure 3:** Conceptual figure showing models with varying relative importance for climate-driven
408 versus dispersal-mediated pathways (as shown on the either sides of the dashed line in the panel)
409 for explaining variation in tail-dependent spatial synchrony in birds' abundance. The model
410 shows the dispersal trait (e.g., hand-wing-index, HWI) and tail-dependent spatial synchrony in
411 climate (e.g., temperature) can both influence tail-dependent spatial synchrony in abundance.

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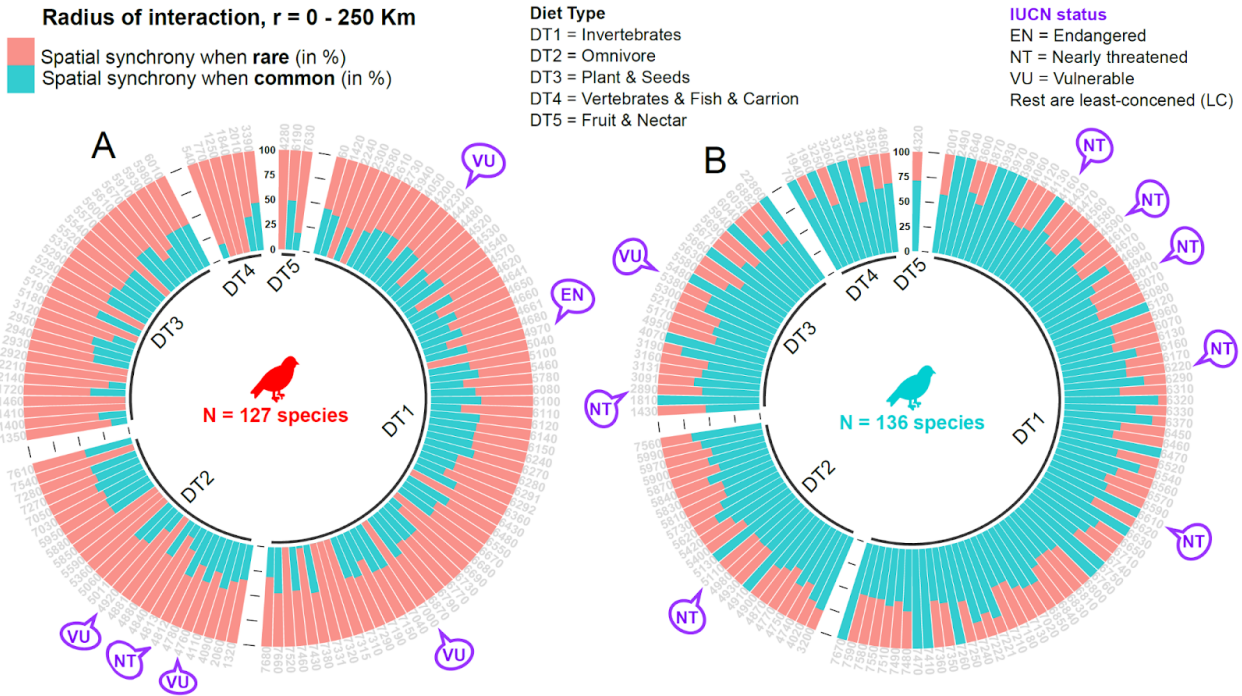
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420 **Figure 4:** Tail-dependence patterns in spatial synchrony of birds' abundance within 0-250 Km
 421 between-sites distance (A) when species are rare (lower tail-dependent, Case I of Fig. 2, A), and
 422 (B) when species are common (upper tail-dependent, Case II of Fig. 2, A). Each bar in the
 423 circular stacked barplots are color-coded based on the proportion of lower-tail dependence
 424 $f_{TD,L}^{abundance}$ (in red) and upper-tail dependence $f_{TD,|U|}^{abundance}$ (in blue) in abundance multiplied by 100
 425 to show in percentage. In (A) 127 species show higher proportion in red than blue color meaning
 426 that those species are showing more lower-tail dependent spatial synchrony in abundance. In (B)
 427 136 species show more upper-tail dependent spatial synchrony in their abundance. The numeral
 428 code written in gray on top of each bar is the AOU code for each species (can be found from the
 429 complete species list as supplied with BBS data (Pardieck *et al.* 2020), we also provide the info
 430 for 263 species as a csv file in the "RESULTS" folder of the code repository). There are five
 431 categories based on diets (DT1: invertebrates, DT2: omnivore, DT3: plants & seeds, DT4:
 432 vertebrates & fish & carrion, DT5: fruit & nectar) and four categories based on IUCN status

433 (endangered: EN, nearly threatened: NT, vulnerable: VU, and least concerned: LC). No clear
434 pattern found for either of the categories. However, many species in the LC category exhibit
435 synchronously rare abundances across sites.

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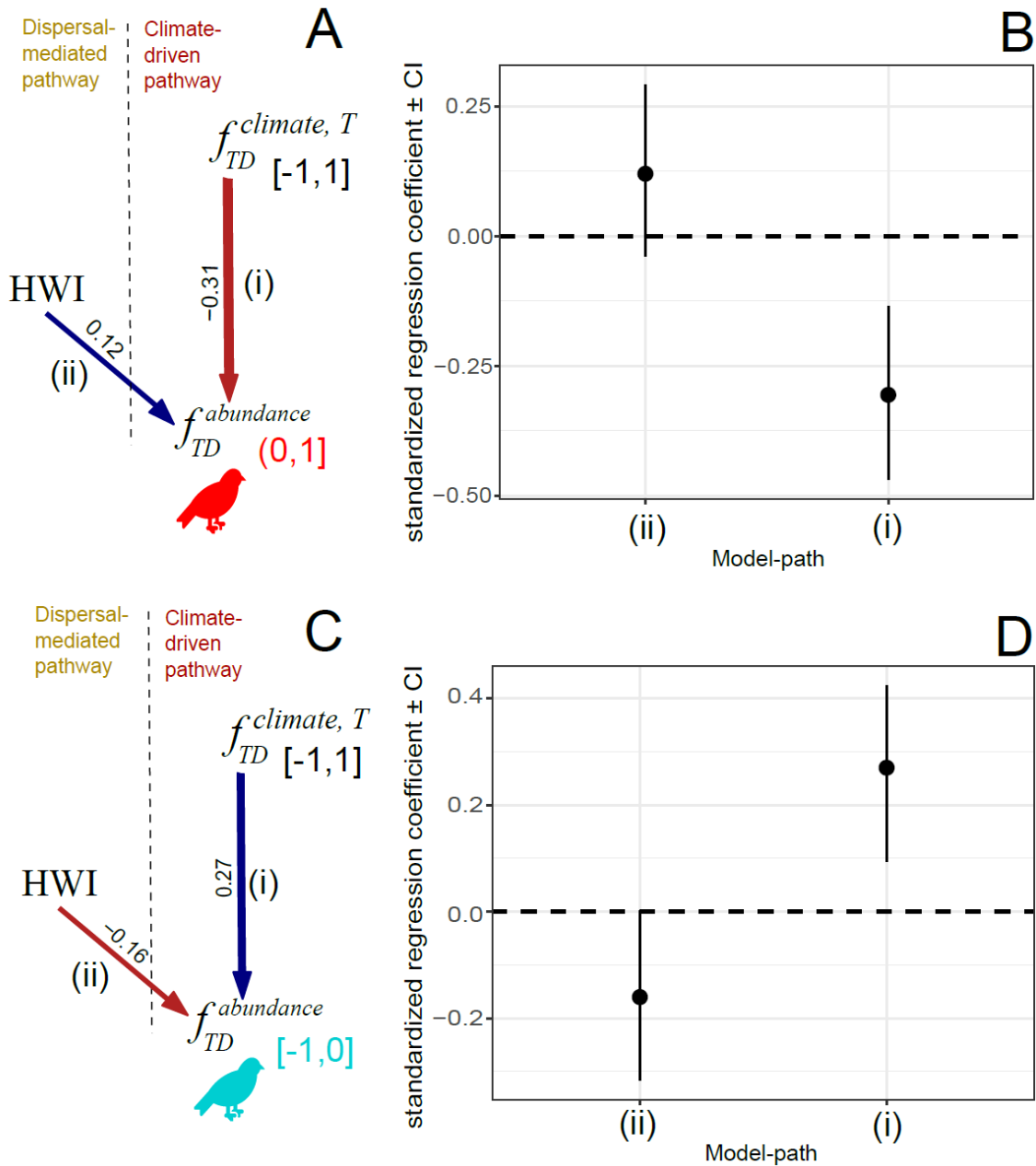
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457 **Figure 5:** Model results from phylogenetic path analysis. (A, B) Model results for 124 bird
 458 species that show synchronously low abundance across sites; proportion of tail-dependent spatial
 459 synchrony in abundance, $f_{TD}^{abundance}$ here has a range (0, 1]. (C, D) Model results for 129 bird
 460 species that show synchronously high abundance across sites; proportion of tail-dependent
 461 spatial synchrony in abundance, $f_{TD}^{abundance}$ here has a range [-1, 0). (A, C) are path diagrams for

462 those two group of species showing the relative importance of climate-driven (via $f_{TD}^{climate,T}$)
463 versus dispersal-mediated (via dispersal trait hand-wing-index HWI) pathways (also see Fig. 3).
464 (B, D) show the summarised path-estimates and confidence interval (CI) from 1,000 bootstraps
465 for those two groups. If the bar crosses the horizontal dashed line at $y=0$, then that is not
466 significant. Models' goodness of fit test were checked with p-value from C-statistic: in both
467 cases it was >0.05 (for A-B: C-statistic=4.66, $p=0.09$; for C-D: C-statistic=0.621, $p=0.733$).

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